Nature Conservation

Nature Conservation 61: 95–111 (2026)
DOI: 10.3897/natureconservation.61.146507

Research Article

Behavioural responses of fireflies to artificial light: red lights attract adult *Lamprigera* (Coleoptera, Lampyridae)

Fathan Anandadzikra Muharraran[1], Wei Jack Tan[1], Wan Faridah Akmal Jusoh[1]

1 *School of Science, Monash University Malaysia, Selangor, Malaysia*
Corresponding author: Wan Faridah Akmal Jusoh (wanf.ajusoh@monash.edu)

Abstract

Artificial lights expanding into natural environments disrupt ecological systems, affecting organisms that depend on natural light cues. Fireflies, which use bioluminescence for communication, are especially vulnerable. Although red light has been suggested as a solution, its effectiveness varies. This study examines how adult male and larval *Lamprigera* fireflies respond to varying intensities of artificial light at different wavelengths. We conducted field observations on adult male attraction patterns and *ex situ* studies of larval behaviour. Adult males were attracted to red and warm-white light, whereas larvae showed no response to red light or low-intensity light. Higher-intensity warm-white and cool-white light suppressed overall larval activity, with increasing intensity amplifying negative impacts regardless of spectral composition. Our findings indicate that successful light mitigation strategies for fireflies require balancing life stage-specific responses while maintaining artificial light intensities that minimise ecological impacts yet preserve human visual function.

Key words: Bioluminescence, crepuscular, light intensity, light pollution, light spectra, mating, nocturnal ecology, phototaxis

OPEN ACCESS

Academic editor: Reinhard Klenke
Received: 11 January 2025
Accepted: 23 October 2025
Published: 9 January 2026

ZooBank: https://zoobank.org/95FA47B9-0178-44CD-8118-FF4B846B77CE

Citation: Muharraran FA, Tan WJ, Jusoh WFA (2026) Behavioural responses of fireflies to artificial light: red lights attract adult *Lamprigera* (Coleoptera, Lampyridae). Nature Conservation 61: 95–111. https://doi.org/10.3897/natureconservation.61.146507

Copyright: ©
Fathan Anandadzikra Muharraran et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Urban areas are expanding into pristine environments to accommodate the demands of a gradually growing urban population (United Nations Department of Economic and Social Affairs 2019; Nuissl and Siedentop 2021). One often overlooked consequence of urbanisation is the introduction of artificial lights, which alter the natural night sky and lead to light pollution (Cheon and Kim 2020; Theodorou 2022). Since ecological systems are organised by daily light–dark cycles (Bradshaw and Holzapfel 2010; Kronfeld-Schor et al. 2013), brightening naturally dark areas and blurring the transition from light to dark through artificial lights at night (ALAN) can negatively affect organisms that depend on light cues (Gaston et al. 2013; Gaston et al. 2014; Owens and Lewis 2018). Biological mechanisms often use light as a source of information, where its direction, duration, and spectral composition can inform organisms of their location, time, and surrounding characteristics (Ragni and Ribera D'Alcalà 2004; Gaston et al. 2013). Consequently, altering natural light profiles can mislead organisms, affecting intrinsic behaviours such as navigation, foraging, predator avoidance, timing of reproduction, and selection of mating partners (Gaston et al. 2013).

Fireflies, which have adapted bioluminescence as a unique form of reproductive communication and warning display (Branham and John 2001; Martin et al. 2016), are obvious victims of the effects of artificial light (Owens et al. 2022; Ghosh et al. 2024). Indeed, ALAN has been identified as a leading factor in the decline of firefly populations (Lewis et al. 2020; Owens et al. 2020, 2022). Exposure to artificial light, particularly at short wavelengths, inhibits firefly signalling activity (Owens et al. 2018; Hillón-Salas et al. 2024). For glow-worm fireflies, characterised by their constant glow and wingless adult females (Lewis 2009), exposure to intense artificial light suppresses their bioluminescent glow (Mbugua et al. 2019; Elgert et al. 2020). Given that courtship displays are essential for the mating success of adult nocturnal fireflies (Demary et al. 2006), this suppression of bioluminescence reduces their attractiveness to mates and decreases their visibility, thereby leading to reduced mating behaviour (Elgert et al. 2020; Owens and Lewis 2022).

Several studies have recommended the use of long-wavelength red light to mitigate the adverse effects of light pollution while maintaining human visual performance in low-light conditions (Long et al. 2022; Kivelä et al. 2023; Longcore 2023). This approach has gained traction in Europe, where red lights are being promoted in outdoor areas (Bat Conservation Trust 2023; Selux 2024). While this implementation initially targeted the mitigation of artificial light effects on bats (Bat Conservation Trust 2023), long-wavelength red light is generally found to have the least harmful impact across several taxonomic groups (Longcore 2023), including nocturnal insects (Owens and Lewis 2018). This reduced impact is often attributed to either the organism's inability to perceive long-wavelength light or its particular sensitivity to short-wavelength light (Owens et al. 2018; Longcore 2023).

Studies have shown that, for fireflies, exposure to long-wavelength light does not significantly affect their communication or mate-attraction capabilities (Owens et al. 2018; Kivelä et al. 2023). However, the impact of light pollution on insect ecology is complex and multifaceted (Owens and Lewis 2018). While a transition towards long-wavelength red light demonstrates the potential to mitigate the adverse effects of ALAN for certain species, it may inadvertently lead to detrimental effects on others (Owens and Lewis 2018; Briolat et al. 2021). For instance, long-wavelength light can inhibit flower colour perception in hawkmoths (Briolat et al. 2021) and reduce populations of pea aphids by inhibiting the flowering of host plants (Bennie et al. 2015). Even among fireflies, male glow-worms in the genus *Diaphanes* found in Rwanda have shown attraction to red light (Yelena et al. 2016), which could disrupt their mating success (Elgert et al. 2020; Owens and Lewis 2022).

A comprehensive understanding of firefly behavioural responses to different ALAN exposures is essential for evaluating the effectiveness of light pollution mitigation strategies. However, there are gaps in our current knowledge, especially in our understanding of the effects of long-wavelength red light. While Yelena et al. (2016) observed the attraction of *Diaphanes* sp. to red lights, their observation was limited to only three nights of data collection with a single trap and no control; thus, the study requires further validation. Furthermore, studies that have examined the impact of red light (Owens et al. 2018; Owens and Lewis 2022; Kivelä et al. 2023) often fail to consider the effects at different light intensities, even though recent research suggests that artificial light at high intensities has a significant influence on

behavioural responses regardless of spectral composition (Firebaugh and Haynes 2016; Kivelä et al. 2023). Moreover, existing behavioural studies have predominantly focused on adult fireflies (Owens et al. 2022), despite larvae representing the majority of a firefly's life cycle (Riley et al. 2021). Preliminary observations by Mbugua et al. (2019) found *Lamprigera* sp. larvae to become immobilised when exposed to intense artificial light, suggesting the inability of firefly larvae to adapt spatially to the impacts of ALAN (Elgert et al. 2020). However, empirical evidence supporting this observation remains lacking, and larval behavioural responses to long-wavelength red light are unexplored (Mbugua et al. 2019; Elgert et al. 2020; Owens and Lewis 2022).

Given these knowledge gaps, *Lamprigera* presents a model species for investigation. This genus is notable for its large size (Fig. 1) (McDermott 1964). It is characterised by a bright, continuous green glow and sexual dimorphism involving neotenic female adults that retain juvenile characteristics (Brues 1941). The adults are crepuscular and active only during twilight (Jeng et al. 2007), whereas their larvae are nocturnal and become active later at night. In Peninsular Malaysia, *Lamprigera* is typically found in hilly regions such as Fraser's Hill in Pahang (Nada and Ballantyne 2021) but demonstrate resilience to human disturbances, as populations persist in urban parks near the megacity of Kuala Lumpur, such as Bukit Kiara (Mbugua et al. 2019). Despite their unique characteristics and urban adaptability, *Lamprigera* remains understudied compared with other firefly genera, with specimens in Bukit Kiara not yet identified to the species level.

The objective of this research was to determine how varying artificial light exposure affects the intrinsic behavioural responses of fireflies at different life stages through controlled *in situ* and *ex situ* observation experiments.

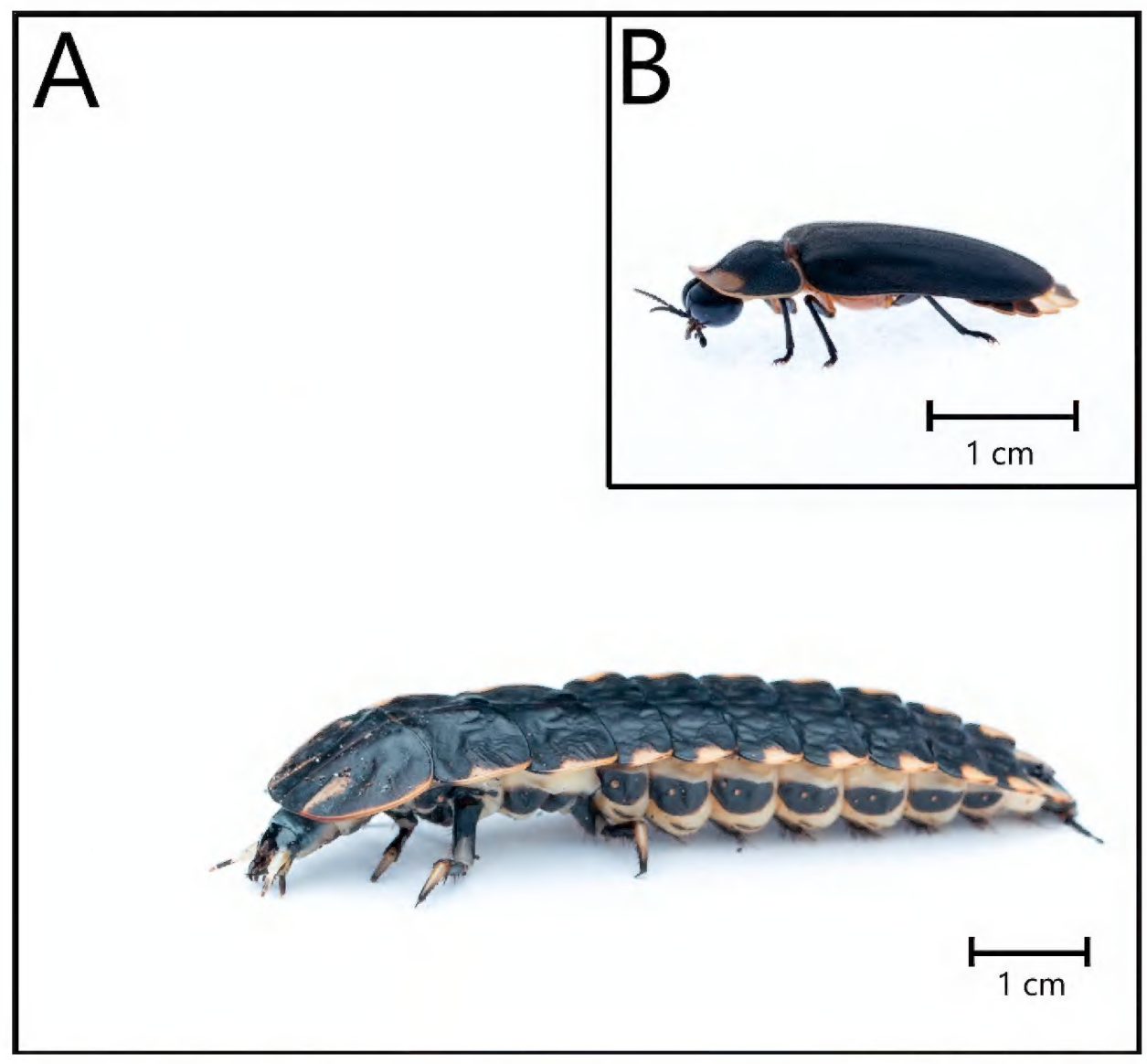

Figure 1. *Lamprigera* sp. from Bukit Kiara. **A.** Larva; **B.** Adult male. Photographed by Nicholas HL Tan.

We investigated the behavioural responses of the glow-worm firefly *Lamprigera* to artificial light exposure across three spectral ranges – red, warm-white, and cool-white – at varying intensities. *In situ* observations were conducted to assess adult male behavioural responses by quantifying both their presence and attraction towards the light source in an artificially illuminated plot. Larval responses were evaluated through *ex situ* laboratory observations, measuring behaviour based on spatial positioning, bioluminescent display times, directional movement, and overall movement activity. We hypothesised that *Lamprigera* would exhibit different responses to different light exposures, with some responses being spatially adaptive through movement away from light sources or by seeking shelter under shade.

Methods

Study organism

Lamprigera fireflies found in Bukit Kiara served as our study organism. Although they have not been identified to the species level, no discernible morphological differences were observed among those examined to suggest multiple species. Therefore, all were treated as a single species for this study. The green glow of their larvae has a peak wavelength of 556 nm, as measured with a spectrophotometer (Lightning Passport Spectrometer, Asensetek), as shown in Fig. 2.

For the *ex situ* larval observation, a total of 43 *Lamprigera* larvae were collected at Bukit Kiara from November 2023 to April 2024, with collection occurring the night before each experiment to allow for acclimation. Larval body lengths ranged from 3 to 9 cm, with an average length of 5.7 ± 1.6 cm. Each larva was transported in an insect cage containing leaves and TRIO Growmate Eazy Mix (a soil mixture of peat moss, fertiliser, and compost). In the laboratory, a thermostat maintained room and soil temperatures at 24.41 °C and 24.52 °C, respectively. Daily spraying maintained humidity at 95.89%, and a timed light switch controlled an Exo Terra Natural Light bulb to simulate a daylight cycle from 6:00 to 19:00. The bulb was designed to emit full-spectrum light, approximating the spectrum of natural daylight. Larvae were released back to Bukit Kiara the night after experimentation.

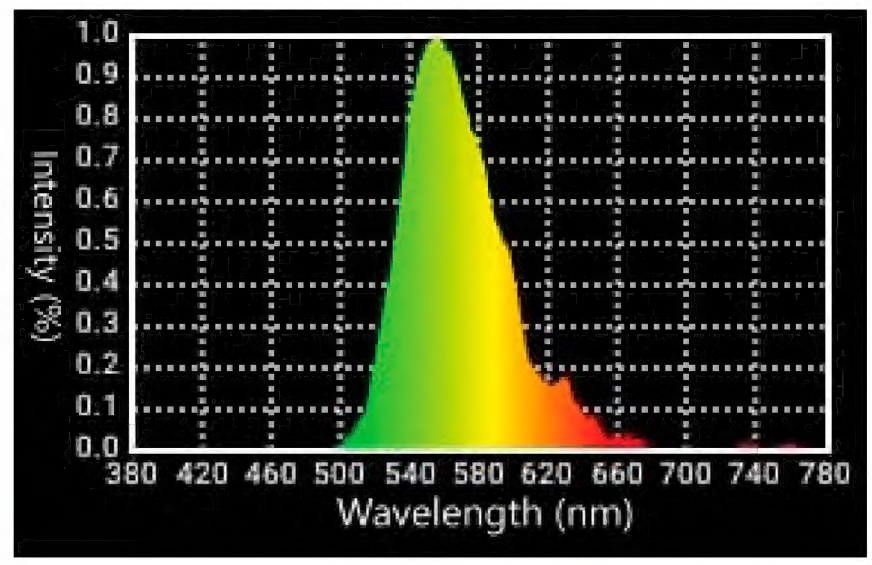

Figure 2. Spectral characteristics of larval glow as measured with a spectrophotometer. Spectral distributions are plotted with relative intensity (percentage) against wavelength (nm). A single dominant peak was exhibited at 556 nm (100% intensity).

Artificial lights

Artificial light was simulated using an RGB LED wired into an Arduino Kit circuit board and encased in a cardboard box. The LED was set to emit light at two levels of brightness, 1× (100 ± 20 lux) and 0.1× (10 ± 2 lux), as measured at 1 cm distance with a light meter, representing regular and dim lighting conditions, respectively, at factors of 10. The 1× brightness level approximated the measured brightness of streetlights in Bukit Kiara at ground level. Three common commercially available colours were used: red (peak at 630 nm), warm-white (peaks at 580 and 470 nm), and cool-white (peaks at 550 and 470 nm), as measured with a spectrophotometer (Fig. 3). For the *ex situ* larval observation, an additional level of brightness was introduced at 10× (1000 ± 200 lux) to observe larval responses under extreme light conditions.

In situ adult male *Lamprigera* observation

The experiment was conducted along a randomly selected forest trail in Bukit Kiara (3.1519232N, 101.6375516E). The study site is a relatively undeveloped secondary forest habitat with minimal human disturbance beyond the cleared trail pathway. The clearing leaves the location relatively open, but the surrounding area remains dense with foliage from shrubs and canopy trees (Fig. 4). Each replicate started at sunset (which varied from 18:50 to 19:20, depending on the date). For 20 minutes, the LED light was placed at the forest trail location, where it was turned on during the light treatments or turned off during

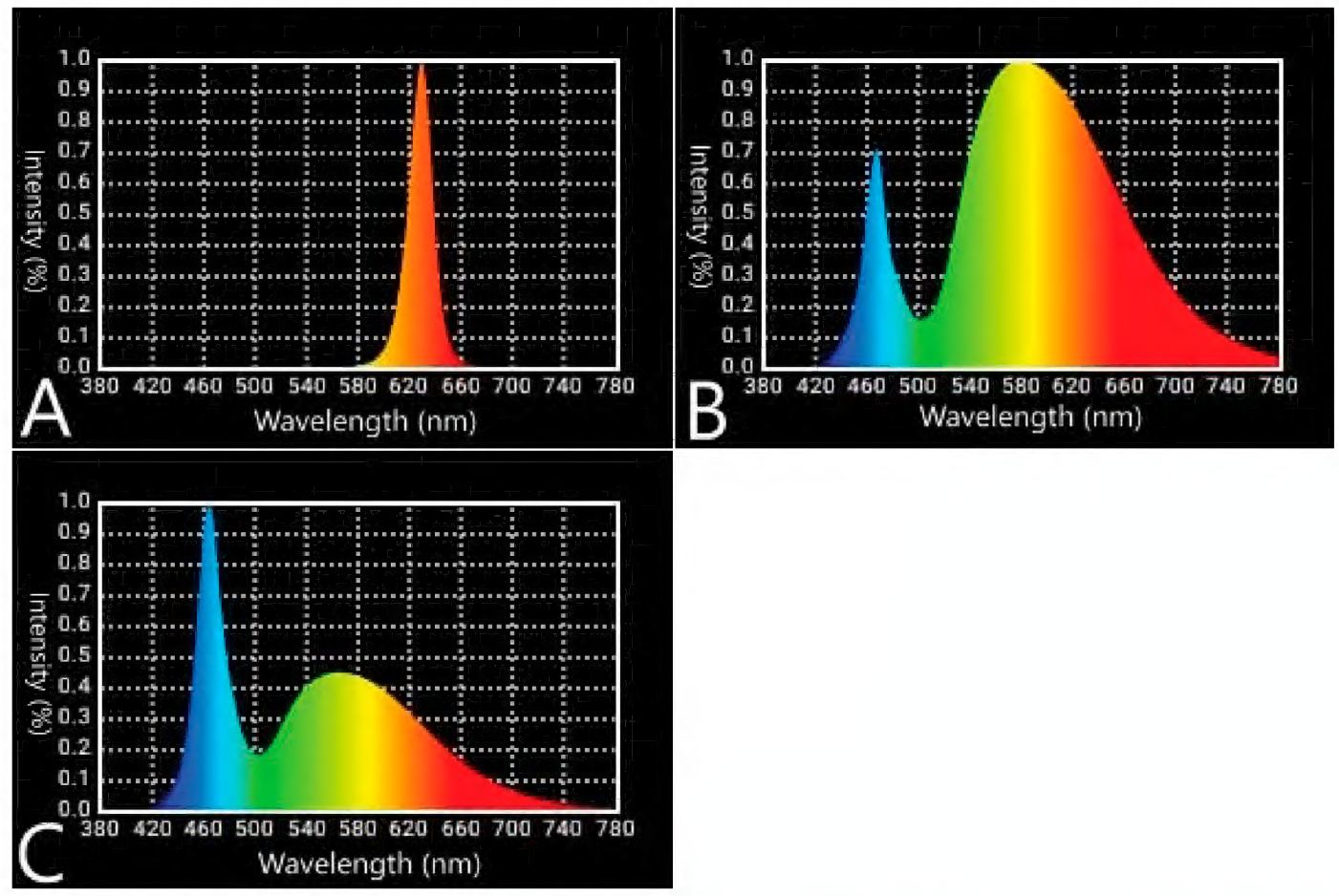

Figure 3. Spectral characteristics of the experimental LED light source as measured with a spectrophotometer. **A.** Red light; **B.** Warm-white; **C.** Cool-white. Spectral distributions are plotted with relative intensity (percentage) against wavelength (nm). Red exhibits a single peak at 630 nm (100% intensity). Warm-white exhibits two peaks, a primary peak at 580 nm (100% intensity) and a secondary peak at 470 nm (70% intensity). Cool-white also exhibits two peaks, a primary peak at 470 nm (100% intensity) and a secondary peak at 550 nm (45% intensity).

Figure 4. *In situ* experiment site in Bukit Kiara during the day. Photographed by Fathan A. Muharraran.

the control (Fig. 5). During the experimental period, adult male *Lamprigera* observed within 5 m of the device were tallied. If an individual flew towards the LED light and attached itself to the light for over 30 seconds, this behaviour was scored as attraction towards the LED light. As adult males were not individually marked, there was a potential overestimation of the actual number of individuals; however, this procedure was applied consistently across all replicates and treatments. The proportion of individuals attracted to the LED over the total observed per replicate was calculated to determine whether artificial light emitted by the LED device could attract adult males. The frequency of adult males and the proportion of attraction under different light conditions were then compared with the control. To ensure no other compounding variables, temperature and humidity were measured with a weather meter (Kestrel 3500 Weather Meter), and the brightness of the area with a light meter (Pro'sKit MT-4007 Light Meter), before and after each experiment.

Ex situ larval *Lamprigera* observation

The experiment adopted a modified methodology (Elgert et al. 2020), utilising a 120 cm × 15 cm box with an LED attached to the 120 cm end, as shown in Fig. 6. The box contained leaves and a 5 cm layer of TRIO Growmate Eazy Mix. Similar to the *in situ* observation, the LED light emitted the same brightness and colours, except for an additional brightness level of 10×. The experiment was conducted between 19:40 and 20:40, during which a larva was placed at the centre of the box, and its position and behaviour were recorded every 5 minutes. Observed behaviours were characterised as locomotor behaviour (stationary or moving, and direction of movement relative to the light source) and signalling behaviour (whether the light organ was luminescent). The position

Figure 5. An LED light device placed at the experiment site in Bukit Kiara. Photographed by Fathan A. Muharraran.

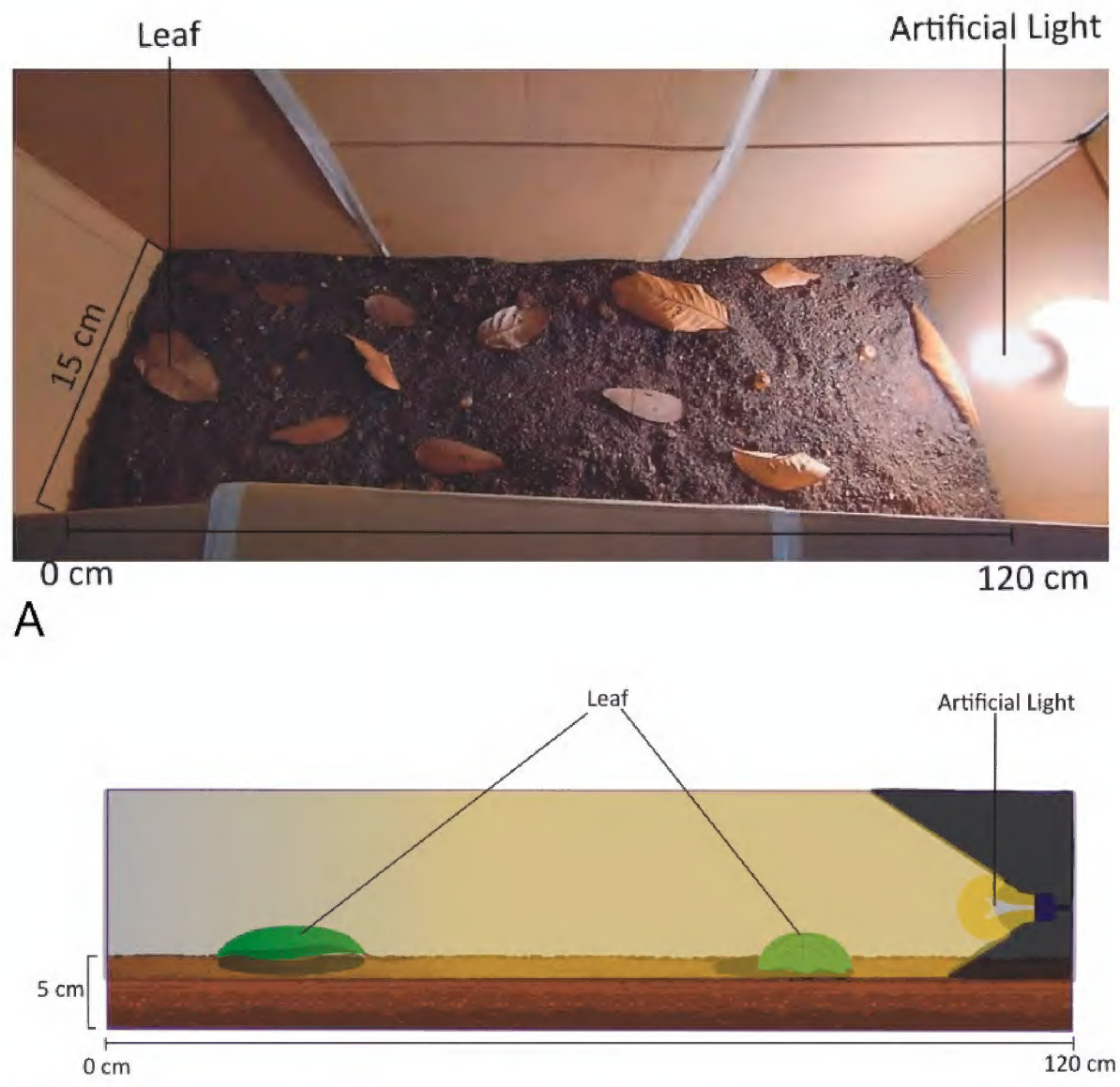

Figure 6. Box set-up for *ex situ* observation from different views. **A.** Top-down view; **B.** Schematic oblique-lateral view. Image made by Fathan A. Muharraran.

was recorded based on horizontal positioning (whether in the open or under an object) and vertical positioning (above or below soil level). Data were summarised by calculating the proportion of time a particular behaviour or position

was displayed during the entire duration of the experiment. This allowed categorical data on larval behaviour and position to be quantified as a percentage. Position data were then spatially mapped as percentages, while behavioural data were transformed into linear data using a probit transformation to allow statistical analysis (Bliss 1934; Wadley 1952). Position and behavioural proportion data under different light conditions were then statistically compared with the control to determine whether different exposures to artificial light would evoke behavioural responses in *Lamprigera* sp. larvae.

Data analysis

Between November 2023 and April 2024, a total of 36 *in situ* experiments were conducted, with five replicates for each light treatment and six replicates for the control. For the *ex situ* study, 43 experiments were conducted, with 4–5 replicates for each light treatment and five replicates for the control. A Wilcoxon rank-sum test was performed to determine the difference in *Lamprigera* firefly behaviour between all light treatments and the control, under the null hypothesis that there is no significant impact of differential light intensities on larval behaviour.

Results

Behavioural responses of adult males to artificial lights

Significantly more adult male *Lamprigera* were observed in the area during exposure to artificial light at red and warm-white spectra compared with control conditions (Table 1; red: p = 0.007 and 0.006 for low and high intensities, respectively; warm-white: p = 0.019 for both intensities), whereas cool-white light showed no significant difference. Attraction behaviour was observed under red and warm-white light exposure (Table 1; red: p = 0.005 and 0.006 for low and high intensities, respectively; warm-white: p = 0.009 for both intensities), with higher attraction rates under red light (97.1% and 85.2% at low and high intensities) compared with warm-white light (43.9% and 51.4% at low and high intensities). Although increased light intensity corresponded to higher numbers of adult males observed (red: 7.2 to 16.4; warm-white: 6.8 to 11), it did not correlate with increased attraction rates. At least one adult male attracted to the artificial lights was observed extending its abdomen and exposing its genitalia towards the LED light (Fig. 7) before flying away.

Table 1. Summary of *in situ* behavioural responses of adult males to artificial lights under different light conditions.

Replicates	Light Treatment		Males observed		Proportion of males attracted to artificial light	
	Light colour	Light intensity	Mean ± SD	p-value	Mean ± SD	p-value
6	Control	-	1.8 ± 0.5	-	0.000 ± 0.000	-
5	Red	Low	7.2 ± 3.8	0.007	0.971 ± 0.063	0.005
5	Red	High	16.4 ± 9.3	0.006	0.852 ± 0.203	0.006
5	Warm-white	Low	6.8 ± 5.4	0.019	0.439 ± 0.281	0.009
5	Warm-white	High	11 ± 9.4	0.019	0.514 ± 0.393	0.009
5	Cool-white	Low	0.2 ± 0.5	0.080	0.200 ± 0.500	0.116
5	Cool-white	High	0.6 ± 1.2	0.520	0.000 ± 0.000	0.584

Footnote: Standard deviation (SD).

Figure 7. An adult male *Lamprigera* sp. extending its abdomen and exposing its genitalia towards an LED emitting warm-white light from the experimental LED device. Photographed by Wei Jack Tan.

Larval behavioural responses to artificial lights

Exposure to warm-white and cool-white artificial light at high and very high intensities significantly reduced larval movement (Table 2; warm-white: $p = 0.028$ and $p = 0.004$ for high and very high intensities, respectively; cool-white: $p = 0.007$ and $p = 0.008$ for high and very high intensities, respectively). Bioluminescent activity decreased under similar conditions, except under warm-white light at high intensity (Table 2; warm-white: $p = 0.004$ for very high intensity; cool-white: $p = 0.041$ and $p = 0.012$ for high and very high intensities, respectively). Movement direction and leaf-settling behaviour remained unaffected across all light conditions, except under very high-intensity cool-white light, where a significant proportion of larvae were observed moving underground (42.3% compared with 0%; $p = 0.035$). Red light across all intensities and low-intensity light across all wavelengths did not significantly affect larval behaviour. Increasing light intensity from high to very high corresponded to decreased movement (warm-white: 29.1% to 10%; cool-white: 17.4% to 5.4%; red: 67.1% to 55.1%) and reduced bioluminescent activity (warm-white: 66.7% to 17.2%; cool-white: 40.9% to 25.6%; red: 89.3% to 49.1%) across all wavelengths.

Table 2. Summary of *ex situ* behavioural responses of larvae to artificial lights under different light conditions.

Light condition		Movement		Movement away from light		Under a leaf		Aboveground		Glowing	
Light colour	Light intensity	Proportion	p-value	Proportion	p-value	Proportion	p-value	Proportion	p-value	Proportion	p-value
Control	Control	0.661	-	0.533	-	0.286	-	1.000	-	0.837	-
Red	Low	0.684	1.000	0.659	0.571	0.484	0.256	1.000	1.000	0.865	0.699
Red	High	0.671	0.685	0.623	0.570	0.308	0.807	0.971	0.568	0.893	0.122
Red	Very High	0.551	0.345	0.700	0.305	0.120	1.000	0.926	0.121	0.491	0.217
Warm-white	Low	0.482	0.515	0.707	0.850	0.452	0.744	1.000	0.187	0.797	0.568
Warm-white	High	0.291	0.028	0.527	0.186	0.468	0.29	0.901	0.118	0.667	0.288
Warm-white	Very High	0.100	0.004	0.800	0.186	0.364	0.684	0.647	0.152	0.172	0.004
Cool-white	Low	0.465	0.167	0.526	0.808	0.205	0.935	1.000	0.802	0.612	0.176
Cool-white	High	0.174	0.007	0.415	0.569	0.510	0.221	1.000	0.802	0.409	0.041
Cool-white	Very High	0.54	0.008	0.750	1.000	0.000	0.255	0.577	0.035	0.256	0.014

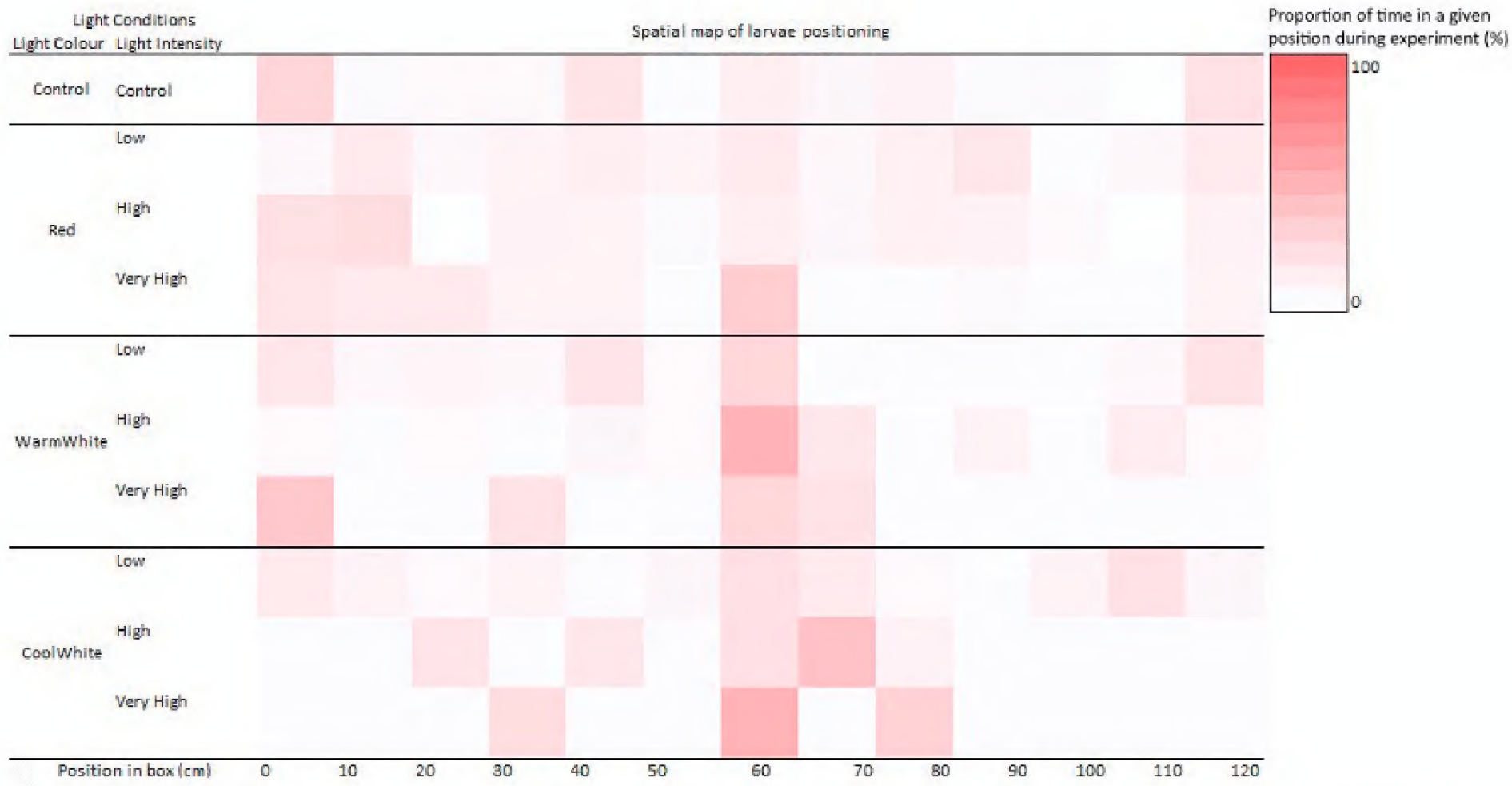

Figure 8. Spatial heat map representing the spatial distribution of larvae under different light conditions in the experimental set-up.

Positional heat maps, where heat intensity represents the proportion of time larvae were observed at a particular position, revealed that *Lamprigera* larvae exhibited continuous movement throughout the experimental arena under control conditions, red wavelength exposure at all intensities, and low-intensity exposure across all wavelengths (Fig. 8), showing uniform spatial heat distribution. In contrast, under high- and very high-intensity warm-white and cool-white light, larvae predominantly remained stationary at the mid-point position (60 cm), with intermittent bidirectional movement resulting in discontinuous heat signatures, as shown in Fig. 8.

Discussion

The present research demonstrates that adult males of *Lamprigera* sp. are attracted to red and warm-white artificial light exposure, often characterised by the extension of the abdomen and the exposure of the genitalia towards the LED light. This behaviour, also documented by Yelena et al. (2016), suggests an attempted mating response in which males were misled by artificial lights, mistaking them for female bioluminescent signals. We also observed that the males quickly departed after a brief period of manipulating their genitalia towards the LED light, seemingly realising that they were engaging not with a female, but with an object that mimicked female cues. This finding may indicate an adaptive capacity to distinguish or discriminate non-biological light sources. However, multiple visits by the same individual could not be excluded from our observation. Studies have shown that fireflies such as *Aquatica ficta* and *Lampyris noctiluca* are unresponsive to red wavelengths due to their inability to perceive long wavelengths above 597 nm (Owens et al. 2018; Kivelä et al. 2023). Thus, we suspect that the consistent attraction of *Lamprigera* sp. towards red light indicates an inability to discriminate between red and green wavelengths. This poor spectral discrimination may result from sharing

a single photoreceptor for red and green wavelengths (Briscoe and Chittka 2001), consistent with nocturnal insects typically prioritising light sensitivity over spectral discrimination (Feuda et al. 2016; Tierney et al. 2017). Given that *Lamprigera* sp. emit a green glow (556 nm), males are likely to perceive the red spectrum from red and warm-white artificial light as potential mate signals. The more consistent attraction of adult males under red light compared with warm-white light is likely caused by the additional blue peak (470 nm) present in the warm-white spectrum, which is known to have detrimental effects on insects (Shibuya et al. 2018). Short-wavelength exposure below 533 nm has been associated with reduced signalling behaviour (Booth et al. 2004; Owens et al. 2018; Shibuya et al. 2018), decreased mate-attraction success (Elgert et al. 2020; Owens and Lewis 2022; Kivelä et al. 2023), and impaired larval development (Chen et al. 2021). This wavelength sensitivity explains the absence of attraction under cool-white light, which contains the most intense blue component (560 nm). Furthermore, increased light intensity corresponded with higher male abundance, suggesting sexual selection for signal brightness (Hopkins et al. 2015; Elgert et al. 2021). However, attraction rates decreased, which we suspect is due to visual impairment as males approach intense artificial light. Future research should test additional light intensities to establish correlative relationships and validate these findings.

Unlike adult males, *Lamprigera* sp. larvae showed no response to red light. We attribute this difference to simpler larval visual systems consisting of bilateral stemmata compared with the larger, more complex eyes of adult males (Murphy and Moiseff 2019). The rudimentary larval visual structure may limit their ability to perceive long wavelengths (Owens et al. 2018). Similarly, larvae showed no behavioural response to low-intensity light across all wavelengths, despite adult male sensitivity at similar intensities. We suggest that this behaviour stems from adaptation to nocturnal illumination during lunar cycles (Williams and Singh 1951; Smolka et al. 2016), allowing larvae to maintain activity despite variations in natural nocturnal brightness. However, high- and very high-intensity warm-white and cool-white light reduced larval movement and glowing activity. Since larval bioluminescence during foraging serves as an aposematic warning to predators (Martin et al. 2017), reduced movement and glowing behaviour correspond to overall lower activity, consistent with previous observations (Mbugua et al. 2019; Elgert et al. 2020). Suppression of activity under intense artificial light suggests disrupted photoperiod detection and circadian rhythms (Owens and Lewis 2018; Mbugua et al. 2019), causing larvae to remain inactive as if it were daytime. Observed intermittent activity may reflect larvae attempting to seek darker habitats before returning to inactivity until light exposure decreases. Similar to the response of adult males, cool-white light suppressed larval activity more than warm-white light, with stronger impacts at higher intensities for both exposures. This suppressive effect likely stems from the blue spectral peaks present in both lights, either through their lethal effects (Shibuya et al. 2018) or their similarity to daylight spectra (Elvidge et al. 2010).

Regarding spatial adaptive behaviour, larvae showed no consistent patterns across all light conditions, with no significant directional movement away from a light source or shelter-seeking behaviour under a leaf. The observed shelter-seeking behaviour appears to be independent of light exposure, supporting previous findings of maladaptive spatial responses to artificial lights in fireflies (Elgert

et al. 2020). We suggest that the absence of directional movement during light exposure may result from two factors: larvae either perceive their immediate location as sufficiently dark and remain stationary without directional preference or experience visual disorientation under intense light that prevents effective navigation away from light. However, larvae demonstrated adaptive capacity through soil-excavating behaviour, but only under very high-intensity cool-white light. This creates a crevice providing shade below ground level, suggesting that this protective behaviour emerges only under extreme light conditions.

In addition, our spatial mapping results, while not statistically significant, indicated subtle signs of light-avoidance behaviour, including movement away from light sources or shelter-seeking under a leaf, especially at high and very high intensities of warm-white and cool-white light. This observation aligns with a previous study on *Photinus* sp. females (Owens and Lewis 2022). The variability in responses observed may reflect individual personality differences, as documented in other insect behavioural studies (Tremmel and Müller 2013). These individual variations in response strategies could explain the lack of statistical significance in our analysis.

The ecological implications of artificial light exposure on *Lamprigera* sp. are substantial. High-intensity warm-white and cool-white lights reduce larval foraging activity and suppress their aposematic bioluminescence, increasing vulnerability to predation (Branham and John 2001; Martin et al. 2016; Mbugua et al. 2019). While red light did not impact larvae, red and warm-white light significantly affected adult males. Given their crepuscular nature, there is a narrow active window approximately 30 minutes long during twilight. Thus, artificial light attraction could critically impair mating success by drawing males away from females and creating potential competition for female signals. Our findings reveal the complexity of developing effective ALAN mitigation strategies. Although adding blue wavelengths can adversely affect larval behaviour, this colour shift reduces artificial light attraction in adult males. However, increasing light intensity – independent of spectral composition – amplifies negative impacts (Firebaugh and Haynes 2016; Kivelä et al. 2023). These findings suggest that artificial lighting solutions for fireflies may still require a blue wavelength component to prevent mating attraction in adults. Nevertheless, maintaining lower light intensities remains critical for minimising the ecological impact of ALAN.

While this research provides insights into *Lamprigera* sp. responses to artificial light, several methodological improvements could be considered for future studies. First, our experimental design utilised directional, horizontally oriented light sources, whereas ALAN in urban environments typically emanates downwards from overhead streetlamps in a more diffused pattern. Future studies should incorporate top-down, diffused lighting to better simulate urban conditions. Second, we did not account for potential spectral contamination through surface reflection – specifically the blue-coloured outer surface of our LED light box in field experiments and the brown-coloured inner surface of our box in laboratory observations – which may have altered the intended spectral composition. Future designs should employ spectrally neutral surfaces or account for reflective interference. Lastly, although we kept larvae under full-spectrum lighting, a more natural approach could involve housing them near windows to simulate natural daylight cycles without artificial light, reducing light exposure prior to experimentation.

Conclusion

This study investigated the behavioural responses of adult male and larval *Lamprigera* fireflies to varying intensities of red, warm-white, and cool-white artificial light through field observations and laboratory experiments. Our findings revealed that different life stages of *Lamprigera* show distinct responses to artificial light, making effective ALAN mitigation strategies for firefly conservation challenging. While red light had a lesser impact on larvae, it disrupted adult male mating behaviour. Therefore, the successful mitigation of light pollution requires careful consideration of both adult and larval developmental stages. We conclude that solutions to the hazards of artificial lighting can be achieved by balancing spectral composition and intensity levels so that ecological impacts are minimised while maintaining adequate visibility for humans.

Acknowledgement

We thank the Friends of Bukit Kiara (FoBK) for their assistance in gaining access to the park and facilitating our early exploration of Bukit Kiara's fireflies. We are grateful to Jabatan Landskap Negara for permitting us to survey the park at night. This project is part of MyABS permit no. 320809. We also thank Dr Sara Lewis for providing valuable feedback on this manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

Funding

This project was funded by the Fundamental Research Grant Scheme (FRGS) awarded by the Ministry of Higher Education, Malaysia (grant code: FRGS/1/2023/WAB11/MUSM/02/1). Analysis of flash patterns was partially supported by the Nagao Natural Environmental Foundation.

Author contributions

Conceptualization: WFAJ. Data curation: FAM. Formal analysis: FAM, WJT. Funding acquisition: WFAJ. Investigation: WJT. Methodology: WJT, FAM. Supervision: WFAJ. Visualization: FAM. Writing - original draft: FAM. Writing - review and editing: FAM, WFAJ.

Author ORCIDs

Fathan Anandadzikra Muharraran https://orcid.org/0009-0007-1653-4997
Wei Jack Tan https://orcid.org/0009-0000-9393-7828
Wan Faridah Akmal Jusoh https://orcid.org/0000-0002-2995-8429

Data availability

All of the data that support the findings of this study are available in the main text.

References

Bat Conservation Trust (2023) Guidance Note GN08/23 Bats and Artificial Lighting At Night. https://theilp.org.uk/publication/guidance-note-8-bats-and-artificial-lighting/

Bennie J, Davies TW, Cruse D, Inger R, Gaston KJ (2015) Cascading effects of artificial light at night: Resource-mediated control of herbivores in a grassland ecosystem. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 370: 20140131. https://doi.org/10.1098/rstb.2014.0131

Bliss CI (1934) The method of Probits. Science 79: 38–39. https://doi.org/10.1126/science.79.2037.38

Booth D, Stewart AJA, Osorio D (2004) Colour vision in the glow-worm *Lampyris noctiluca* (L.)(Coleoptera: Lampyridae): Evidence for a green-blue chromatic mechanism. The Journal of Experimental Biology 207: 2373–2378. https://doi.org/10.1242/jeb.01044

Bradshaw W, Holzapfel C (2010) Light, Time, and the Physiology of Biotic Response to Rapid Climate Change in Animals. Annual Review of Physiology 72: 147–166. https://doi.org/10.1146/annurev-physiol-021909-135837

Branham M, John W (2001) The Evolution of Bioluminescence in Cantharoids (Coleoptera: Elateroidea). The Florida Entomologist 84: 565–586. https://doi.org/10.2307/3496389

Briolat ES, Gaston KJ, Bennie J, Rosenfeld EJ, Troscianko J (2021) Artificial nighttime lighting impacts visual ecology links between flowers, pollinators and predators. Nature Communications 12: 4163. https://doi.org/10.1038/s41467-021-24394-0

Briscoe AD, Chittka L (2001) The evolution of color in insects. Annual Review of Entomology 46: 471–510. https://doi.org/10.1146/annurev.ento.46.1.471

Brues CT (1941) Characteristics of the Larviform Female of the Lampyrid Beetle, Lamprophorus. Psyche (Cambridge, Massachusetts) 48: 060591. https://doi.org/10.1155/1941/60591

Chen YR, Wei WL, Tzeng DTW, Owens ACS, Tang HC, Wu CS, Lin SS, Zhong S, Yang EC (2021) Effects of artificial light at night (ALAN) on gene expression of *Aquatica ficta* firefly larvae. Environmental Pollution 281: 116944. https://doi.org/10.1016/j.envpol.2021.116944

Cheon S, Kim JA (2020) Quantifying the influence of urban sources on night light emissions. Landscape and Urban Planning 204: 103936. https://doi.org/10.1016/j.landurbplan.2020.103936

Demary K, Michaelidis CI, Lewis SM (2006) Firefly Courtship: Behavioral and Morphological Predictors of Male Mating Success in *Photinus greeni*. Ethology : Formerly Zeitschrift für Tierpsychologie 112: 485–492. https://doi.org/10.1111/j.1439-0310.2005.01176.x

Elgert C, Hopkins J, Kaitala A, Candolin U (2020) Reproduction under light pollution: Maladaptive response to spatial variation in artificial light in a glow-worm. Proceedings. Biological Sciences 287: 20200806. https://doi.org/10.1098/rspb.2020.0806

Elgert C, Lehtonen TK, Kaitala A, Candolin U (2021) Sexual selection for bright females prevails under light pollution. Current Zoology 67: 329–331. https://doi.org/10.1093/cz/zoaa071

Elvidge CD, Keith DM, Tuttle BT, Baugh KE (2010) Spectral identification of lighting type and character. Sensors 10: 3961–3988. https://doi.org/10.3390/s100403961

Feuda R, Marlétaz F, Bentley MA, Holland PWH (2016) Conservation, duplication, and divergence of five opsin genes in insect evolution. Genome Biology and Evolution 8: 579–587. https://doi.org/10.1093/gbe/evw015

Firebaugh A, Haynes KJ (2016) Experimental tests of light-pollution impacts on nocturnal insect courtship and dispersal. Oecologia 182: 1203–1211. https://doi.org/10.1007/s00442-016-3723-1

Gaston KJ, Bennie J, Davies TW, Hopkins J (2013) The ecological impacts of nighttime light pollution: A mechanistic appraisal. Biological Reviews of the Cambridge Philosophical Society 88: 912–927. https://doi.org/10.1111/brv.12036

Gaston KJ, Duffy JP, Gaston S, Bennie J, Davies TW (2014) Human alteration of natural light cycles: Causes and ecological consequences. Oecologia 176: 917–931. https://doi.org/10.1007/s00442-014-3088-2

Ghosh S, Chattoraj A, Chakraborty SK (2024) The effect of ALAN on the ecobiological attributes of fireflies (Coleoptera: Lampyridae: Luciolinae): A study from a tropical habitat in India. International Journal of Tropical Insect Science 44: 1159–1184. https://doi.org/10.1007/s42690-024-01202-y

Hillón-Salas JS, Pineda-Dueñas JD, Romero-Chacón AM, Fonseca-Tellez J, Cardona-Restrepo M, Garrido-Villegas SC, Mejía-Tovar D, Arenas-Ríos C, Gaitán-Botero L, Barón-Garzón ZS, Robayo-Salek AF, Pulido-Guarín H, Ovalle-Barrera JJ, Macías-González AD, Bernal-Guatibonza N, Maldonado-Chaparro AA (2024) Artificial light at night reduces flashing in *Photinus* and *Photuris* fireflies during courtship and predation. Journal of Insect Behavior 37: 49–57. https://doi.org/10.1007/s10905-024-09849-8

Hopkins J, Baudry G, Candolin U, Kaitala A (2015) I'm sexy and I glow it: Female ornamentation in a nocturnal capital breeder. Biology Letters 11. https://doi.org/10.1098/rsbl.2015.0599

Jeng ML, Engel MS, Yang P-S (2007) *Oculogryphus*, a remarkable new genus of fireflies from Asia (Coleoptera: Lampyridae). American Museum Novitates 2007: 1–19. https://doi.org/10.1206/0003-0082(2007)3600[1:OARNGO]2.0.CO;2

Kivelä L, Elgert C, Lehtonen TK, Candolin U (2023) The color of artificial light affects mate attraction in the common glow-worm. The Science of the Total Environment 857: 159451. https://doi.org/10.1016/j.scitotenv.2022.159451

Kronfeld-Schor N, Dominoni D, de la Iglesia H, Levy O, Herzog ED, Dayan T, Helfrich-Forster C (2013) Chronobiology by moonlight. Proceedings. Biological Sciences 280: 20123088. https://doi.org/10.1098/rspb.2012.3088

Lewis SM (2009) Bioluminescence and sexual signaling in fireflies. In: Meyer-Rochow VB (Ed.) Bioluminescence in action: A collection of illuminating essays. Research Signpost, India, 147–159.

Lewis SM, Wong CH, Owens ACS, Fallon C, Jepsen S, Thancharoen A, Wu C, De Cock R, Novák M, López-Palafox T, Khoo V, Reed JM (2020) A global perspective on firefly extinction threats. Bioscience 70: 157–167. https://doi.org/10.1093/biosci/biz157

Long TM, Eldridge J, Hancock J, Hirama S, Kiltie R, Koperski M, Trindell RN (2022) Balancing human and sea turtle safety: Evaluating long-wavelength streetlights as a coastal roadway management tool. Coastal Management 50: 184–196. https://doi.org/10.1080/08920753.2022.2022974

Longcore T (2023) A compendium of photopigment peak sensitivities and visual spectral response curves of terrestrial wildlife to guide design of outdoor nighttime lighting. Basic and Applied Ecology 73: 40–50. https://doi.org/10.1016/j.baae.2023.09.002

Martin G, Branham M, Whiting M, Bybee S (2016) Total evidence phylogeny and the evolution of adult bioluminescence in fireflies (Coleoptera: Lampyridae). Molecular Phylogenetics and Evolution 107: 564–575. https://doi.org/10.1016/j.ympev.2016.12.017

Martin GJ, Branham MA, Whiting MF, Bybee SM (2017) Total evidence phylogeny and the evolution of adult bioluminescence in fireflies (Coleoptera: Lampyridae). Molecular Phylogenetics and Evolution 107: 564–575. https://doi.org/10.1016/j.ympev.2016.12.017

Mbugua S, Wong C, Ratnayeke S (2019) Effects of artificial light on the larvae of the firefly *Lamprigera* sp. in an urban city park, Peninsular Malaysia. Journal of Asia-Pacific Entomology 23. https://doi.org/10.1016/j.aspen.2019.10.005

McDermott FA (1964) The Taxonomy of the Lampyridae (Coleoptera). Transactions of the American Entomological Society 90: 1–72. jstor.org/stable/pdf/25077867.pdf

Murphy F, Moiseff A (2019) Anatomy of the stemmata in the Photuris firefly larva. Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology 205: 151–161. https://doi.org/10.1007/s00359-018-01312-2

Nada B, Ballantyne L (2021) Fireflies (Coleoptera: Lampyridae) of Fraser's Hill, Pahang, Malaysia. In: Cheong C, Abidin SZ, Munisha CYN, Bashah RMZRK (Eds) Proceedings of the Fraser's Hill Symposium 2020, December 2020. WWF Malaysia, Malaysia, 86–90.

Nuissl H, Siedentop S (2021) Urbanisation and Land Use Change. In: Weith T, Barkmann T, Gaasch N, Rogga S, Straußß C, Zscheischler J (Eds) Sustainable Land Management in a European Context: A Co-Design Approach. Springer International Publishing, Cham, 75-99. https://doi.org/10.1007/978-3-030-50841-8_5

Owens ACS, Lewis SM (2018) The impact of artificial light at night on nocturnal insects: A review and synthesis. Ecology and Evolution 8: 11337–11358. https://doi.org/10.1002/ece3.4557

Owens ACS, Lewis SM (2022) Artificial light impacts the mate success of female fireflies. Royal Society Open Science 9: 220468. https://doi.org/10.1098/rsos.220468

Owens ACS, Meyer-Rochow VB, Yang E-C (2018) Short- and mid-wavelength artificial light influences the flash signals of *Aquatica ficta* fireflies (Coleoptera: Lampyridae). PLoS ONE 13: e0191576. https://doi.org/10.1371/journal.pone.0191576

Owens ACS, Cochard P, Durrant J, Farnworth B, Perkin EK, Seymoure B (2020) Light pollution is a driver of insect declines. Biological Conservation 241: 108259. https://doi.org/10.1016/j.biocon.2019.108259

Owens ACS, Van den Broeck M, De Cock R, Lewis SM (2022) Behavioral responses of bioluminescent fireflies to artificial light at night. Frontiers in Ecology and Evolution 10: 946640. https://doi.org/10.3389/fevo.2022.946640

Ragni M, Ribera D'Alcalà M (2004) Light as an information carrier underwater. Journal of Plankton Research 26: 433–443. https://doi.org/10.1093/plankt/fbh044

Riley WB, Rosa SP, Lima da Silveira LF (2021) A comprehensive review and call for studies on firefly larvae. PeerJ 9: e12121. https://doi.org/10.7717/peerj.12121

Selux (2024) Biological Red Selux. https://www.selux.com/int/en/circular-light-profiles/biological-red

Shibuya K, Onodera S, Hori M (2018) Toxic wavelength of blue light changes as insects grow. PLoS ONE 13: e0199266. https://doi.org/10.1371/journal.pone.0199266

Smolka J, Baird E, el Jundi B, Reber T, Byrne MJ, Dacke M (2016) Night sky orientation with diurnal and nocturnal eyes: Dim-light adaptations are critical when the moon is out of sight. Animal Behaviour 111: 127–146. https://doi.org/10.1016/j.anbehav.2015.10.005

Theodorou P (2022) The effects of urbanisation on ecological interactions. Current Opinion in Insect Science 52: 100922. https://doi.org/10.1016/j.cois.2022.100922

Tierney SM, Friedrich M, Humphreys WF, Jones TM, Warrant EJ, Wcislo WT (2017) Consequences of evolutionary transitions in changing photic environments. Austral Entomology 56: 23–46. https://doi.org/10.1111/aen.12264

Tremmel M, Müller C (2013) Insect personality depends on environmental conditions. Behavioral Ecology 24: 386–392. https://doi.org/10.1093/beheco/ars175

United Nations Department of Economic and Social Affairs (2019) World Urbanization Prospects: The 2018 Revision (ST/ESA/SER.A/420). https://population.un.org/wup/assets/WUP2018-Report.pdf

Wadley FM (1952) Probit Analysis: A Statistical Treatment of the Sigmoid Response Curve. Annals of the Entomological Society of America 45: 686–686. https://doi.org/10.1093/aesa/45.4.686

Williams CB, Singh BP (1951) Effect of Moonlight on Insect Activity. Nature 167: 853–853. https://doi.org/10.1038/167853a0

Yelena MP, Gavin JM, Seth MB (2016) On the Phototactic Response of Rwandan *Diaphanes* Motschulsky (Coleoptera: Lampyridae) to a Trap with a 630Nm Red Light. Coleopterists Bulletin 70: 559–561. https://doi.org/10.1649/0010-065X-70.3.559